An Exploratory Analysis of Cladistic Relationships within the Superfamily Apoidea, with Special Reference to Sphecid Wasps (Hymenoptera) [1,2]

BYRON A. ALEXANDER

Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, KS 66045, U.S.A.

Abstract.—This paper presents the results of several analyses of cladistic relationships among the sphecid wasps and bees, based on adult and larval morphology, with special emphasis on the tribes of sphecid wasps. The analyses examine the effects of: (1) alternative procedures for determining character polarities, (2) using adult characters alone or both adult and larval characters, (3) analyzing all sphecid tribes or only those tribes for which larvae have been described, and (4) equal weighting of all characters vs. successive approximations character weighting. The monophyly of bees is strongly supported, and the following groups of tribes of sphecid wasps are consistently supported as monophyletic: (a) Ampulicini + Dolichurini; (b) (Sceliphrini + (Sphecini + Ammophilini)); (c) (Aphilanthopini + Philanthini + Cercerini + Pseudoscoliini); (d) (Nyssonini + Gorytini + Stizini + Bembicini). Numerous equally parsimonious resolutions of cladistic relationships among these groups and other sphecid tribes are found.

In 1976, R. M. Bohart and A. S. Menke published a monumental worldwide revision of the genera of sphecid wasps. This encyclopedic compilation of information on the taxonomy, geographic distribution, and external morphology and behavior of adults represents a milestone in our knowledge of these wasps. Another noteworthy feature of this work is its extensive discussions of phylogenetic relationships among sphecid wasps, although its numerous phylogenetic diagrams are not based upon explicitly stated analytical methods. However, Bohart and Menke (1976: Tables 2, 5, 11, 13, 15, 16, 19, and p. 224) present numerous lists of "generalized" and "specialized" states of characters considered to be "of phylogenetic significance" in various groups (usually subfamilies). The implicit message seems to be that the branching diagrams are based upon the characters in these tables. Regardless of how the phylogenetic diagrams may have been derived, the character analyses summarized in the tables do provide the kind of information necessary for a cladistic analysis. Thus, it should in principle be possible to determine how well these characters support the phylogenetic hypotheses presented by Bohart and Menke, and whether there are other phylogenetic hypotheses that would explain the data equally well or better.

A rigorous cladistic analysis requires two types of information in addition to that presented in Bohart and Menke's tables of character states. One is a clear statement of how the characters have been polarized, and the other is a matrix showing the state of each character for each taxon. Bohart and Menke do not present any data matrix in their book, and it is not possible to construct a complete matrix from their descriptions of taxa or discussions of characters. In one of their introductory chapters (p. 29), they do briefly explain how they distinguished between "primitive" and "advanced" states of characters. After discussing the pitfalls of assuming that "simple" characters are primitive and "complex" ones derived, they conclude that "a study of features common in the more primitive hymenopterous families and preserved in some of the Sphecidae is the most productive way of making value judgments on evolutionary paths". This is conceptually close to a method now generally known as outgroup analysis, although more recent formulations of this method (e.g. Watrous and Wheeler 1981, Maddison et al. 1984) are considerably more rigorous and explicit. Bohart and Menke also do not identify which hymenopteran families they consider primitive (relative to sphecid wasps). The first explicit cladistic analysis of aculeate Hymenoptera (Brothers 1975; not cited in Bohart and Menke 1976) presented a hypothesis of the phylogenetic position of sphecid wasps and bees that was quite different from conventional opinion at the time (e.g. Evans and West Eberhard 1970).

Thus, it is not at all certain that the families regarded as primitive by Bohart and Menke would be those selected now in the light of new hypotheses of phylogenetic relationships among aculeate families that have resulted from explicit cladistic analyses (Brothers 1975, Königsmann 1978, Carpenter 1990).

Another important and influential source of information and ideas about sphecid phylogeny has been presented by H.E. Evans and colleagues, in a series of papers describing sphecid larvae and analysing larval characters from a phylogenetic perspective (Evans 1957b, 1958, 1959, 1964a, 1964b, 1966, Evans and Lin 1956a, 1956b, Evans and Matthews 1968). Evans has found larval characters to be most phylogenetically informative for groups that he treats as subfamilies (see especially Evans 1959, 1964). The number of characters employed in his analyses is considerably less than the number of adult characters presented in Bohart and Menke's tables, but a few noteworthy larval characters seem to provide evidence of general patterns of higher-level relationships. The way in which Evans presents and analyzes data on larval characters is very similar to the approach adopted by Bohart and Menke, and the same general remarks on the limitations of this approach apply to both data sets.

The potential importance of larval characters for elucidating higher level phylogenetic relationships among sphecid wasps was recently re-emphasized in a cladistic analysis of the relationships between sphecid wasps and bees published by Lomholdt (1982). He partitions the paraphyletic Sphecidae of Bohart and Menke into two groups that he hypothesizes to be monophyletic. His one synapomorphy for the larger of these groups, which he calls Larridae, is a unique form of the openings of the larval salivary glands. This larval character was also stressed by Evans in his papers, and earlier by Michener (1952).

Many other authors have also been interested in phylogenetic relationships among sphecid wasps, and the preceding discussion is not intended to be an exhaustive historical review of ideas about sphecid relationships. However, the works mentioned above are especially noteworthy because of their comprehensive scope, their thoroughness, and the extent to which they have influenced other workers. Evans and co-workers have published several stimulating and frequently-cited papers discussing general evolutionary patterns among sphecid wasps (e.g. Evans 1957a, 1962, 1966a, 1966b,

1966c, Evans and West Eberhard 1970). In recent years, using phylogenetic patterns deduced from cladistic analyses to inform and evaluate theories about evolutionary processes has been more and more widely advocated as a fruitful research program (Eldredge and Cracraft 1980, Brooks and McLennan 1991, Harvey and Pagel 1991). The growing popularity of this approach makes it even more important to critically assess the strength of evidence supporting published phylogenetic hypotheses. The present paper is a quantitative cladistic analysis of the characters identified in the above-mentioned works of Evans (especially Evans 1959 and 1964a) and of Bohart and Menke (1976).

I did this study as background work for a research project with a narrower focus: a cladistic analysis of the genera in one subfamily, the Philanthinae. Thus, my major objective was to determine whether or not the Philanthinae as defined by Bohart and Menke is monophyletic and to establish its phylogenetic placement within the Apoidea (sensu Michener 1986 and Gauld and Bolton 1988 — i.e., sphecid wasps and bees). Unresolved relationships among taxa not closely related to the Philanthinae did not prevent me from continuing with my study, so I did not attempt to resolve them. A preliminary report of my analysis was published in a newsletter for aculeate researchers (Alexander 1990). I have received several inquiries about that report, and have also given more careful attention to problems involved with outgroup analysis, which have resulted in modified hypotheses of relationships within the Apoidea. The present paper is intended as a more complete presentation of what my exploratory analyses have revealed. Its major conclusion is that much more work remains to be done, but I hope it will also provide a better focus for that future work.

METHODS AND MATERIALS

As explained above, the starting point for this study was a series of tables of polarized characters taken from the works of Bohart and Menke (1976) and Evans (1959). The sphecid wasps belong to a monophyletic group (Apoidea) that also includes the bees (Apiformes). Characters to establish the monophyly of the Apoidea and Apiformes (bees) are based primarily upon Brothers (1975), supplemented by discussions in Bohart and Menke (1976) and Michener (1974).

I have not examined larval specimens myself, so

all my assignments of larval character states to taxa are based upon the literature. In addition to the numerous papers of Evans and co-workers cited earlier, Grandi's (1961) excellent illustrations of aculeate larvae are extremely useful. For bee larvae, I have relied primarily upon the descriptions by McGinley (1987). Evans' polarity assessments for larval characters are used, since information on larval morphology in the outgroup is unfortunately still too fragmentary for meaningful application of more rigorous analytical procedures.

For adult characters, I have examined specimens myself in order to determine the state of each character for each taxon, because such determinations cannot always be made from the literature. I have examined representatives of all the sphecid tribes recognized by Bohart and Menke (1976) and all genera for which both adults and larvae are known, as well as a few representatives of each of the major lineages of bees (traditionally assigned the rank of family). Appendix 1 lists the taxa whose adults I have examined.

In 1984, Day proposed that the puzzling genus *Heterogyna*, which was originally placed in its own monotypic family (Nagy 1969), is an aberrant sphecid wasp. It is not included in most of the analyses presented here, which deal with the taxa treated by Bohart, Menke, and Evans. However, I have recently been able to examine male specimens of four of the five known species of *Heterogyna*, and I accept Day's argument that the males of this genus exhibit the character states that Brothers identified as salient synapomorphies for sphecid wasps and bees, whereas the morphology of females is autapomorphic. I have done one preliminary analysis to determine the phylogenetic position of *Heterogyna* within Apoidea.

The final data matrix (Table 1) consists of ninety characters, of which ten are features of larval morphology, seventy-nine are features of adult morphology, and one is a feature of adult female behavior (character 72 in Table 2, which lists the characters and character states used in all the analyses).

I have selected outgroup taxa from lineages within the Aculeata, as discussed below. Exemplars from the Ichneumonoidea represent an outgroup for the Aculeata, following the unpublished analyses of Mason (1983, cited by Carpenter [1986] and Gauld and Bolton [1988]) which hypothesize that the Aculeata and Ichneumonoidea are sister taxa.

In each of the analyses presented below, a single "hypothetical ancestor" is used as the outgroup for rooting the trees. Different hypothetical ancestors are used in different analyses. This is done to compare the results of analyses based entirely upon Bohart and Menke's judgments about the polarities of adult characters with the results of analyses based upon polarities that are hypothesized according to the procedure outlined by Maddison et al. (1984). The latter procedure determines the most parsimonious distribution of each character on a tree comprised of the ingroup and several outgroup taxa. For each character, this optimized character state distribution is used to hypothesize the state that was present in the ancestor of the ingroup. The tree that forms the basis for this procedure is assumed to be an independent and well-supported hypothesis of phylogenetic relationships among the outgroup taxa. In this type of analysis, the character being "fitted" to the tree is not used to derive the tree.

For my hypothesis, I have used the tree of aculeate relationships in Fig. 2 of Carpenter's (1990) reanalysis of the data in Brothers (1975). In my 1990 report in the newsletter Sphecos, I hypothesized the polarity of each character in my matrix as if the tree derived by Brothers and Carpenter were based upon characters completely independent of those I used in my analysis of relationships within the Apoidea. However, a closer examination of Brothers' data set shows that 23 of the 92 characters that he used in his study are also included in my matrix. Because his hypothesis of aculeate relationships is based on his assessment of the polarity of these characters, it would be logically inconsistent to use his phylogenetic hypothesis to postulate different polarities for these characters. Conflict about the state to be assigned to a given character at a given node — in this case, the node of interest is the common ancestor of the Apoidea — is possible because the most parsimonious distribution of a single character on a predetermined tree will not necessarily correspond to the optimized distribution of that character when it is used in conjunction with a large number of other characters in order to determine the most parsimonious tree for the entire set of characters. Consequently, for the characters in my matrix that Brothers also used in his study, the states that he hypothesized to be the groundplan state for the Apoidea (which he called the Sphecoidea in his paper) are assigned to the hypothetical ancestor in my matrix.

For most characters, the polarities hypothesized

Table 1. Data matrix used in the cladistic analyses. Characters and character states are defined in Table 2. "Outgroup 1" shows the codings used in the preliminary study published in Sphecos (Alexander, 1990), "Outgroup 2" is based on the polarities hypothesized by Bohart and Menke (1976), and "Outgroup 3" is based on the polarities determined by the character state optimization procedure of Maddison et al. (1984). For each taxon entry, the first number is character 0, the last is character 89. A "-" indicates that the character varies within the taxon (for the outgroup, these are characters for which polarity decisions are indecisive), and a "?" indicates that the state is unknown for the taxon (this is primarily used for larval characters, since larvae are undescribed for several taxa). (B and M = Bohart and Menke; optim. = optimized).

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                         0          1          2
Outgroup 1 (Sphecos)  0000000000- 0000000000000- 10-31
Outgroup 2 (B and M ) 0000000- 0000100000000000000- - - -
Outgroup 3 (optim.)   00000000000000000000000010-31
Ampulicini            000001000210000000100000111120
Dolichurini           00000000010000000000200011 11021
Sceliphrini           000001000100000000011- 000000-11
Sphecini              0001111001000 1- 001110000000111
Ammophilini           00011110010011-00-11-000000111
Astatini              000000000000000000111000000031
Pemphredonini         00- 001-00- - 000001-1000010-0-1
Psenini               0010000001020100001- 000010100-
Mellinini             0000000000000000111100000000001
Palarini              10010000110 0-0000011 1000000 110
Miscophini            0000000- 000000000- - 110000-0002
Larrini               101000001000000001011 10000 00000
Trypoxylini           01-0000-0-0-0-01111000000--0-
Crabronini            00100-0-00-0-0001111-000-0--00
Oxybelini             001010000000000001111011001230
Alyssonini            00000000000-0-00-110001111001
Nyssonini             00000000010300000111110 0 01230
Gorytini              00- 000000-00- - - - 011101000-1111
Stizini               001000000100010211101-0010111
Bembicini             10-120200-0000-021110120010111
Aphilanthopini        000001000100011101110000000-11
Philanthini           01010100010001110111000000110
Cercerini             000101000101011101110000010-10
Colletidae            000100000100-110011110000 00110
Andrenidae            000111000100011001110000101110
Halictidae            0-011100010001100111110000-0-10
Melittidae            000111000100011001110000010110
Long-tongued Bees     000131-001000110011100001-110
Laphyragogini         00001000040001100110000000011
Xenospecini           001100010-001-100210000000 10012
Dinetini              001000010000000001111000000 1232
ntomosericini         00110000010000000110000010 0121
Eremiaspheciini       000101000-000000-00000000000011
Odontosphecini        102101000000001001110000010011
Pseudoscoliini        000101000100001101110000010010
Scapheutini           0010010-000-000011100000-0--10
Bothynostethini       00- - 010-0-0000001111000100010
Heterogyna            00000000000000000011100010 0002
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                         3          4          5
Outgroup 1 (Sphecos)  0-0-02000- 0000000-000100000000
Outgroup 2 (B and M ) 0- 0022000001000-000101000000000
Outgroup 3 (optim.)   01000200010000000-0-0100000000
Ampulicini            2001000101000100020220111010011 1
Dolichurini           21011000000000000022011 10000011
Sceliphrini           00001000001000011001011 10000011
Sphecini              00011000011-000110010110-0--10
Ammophilini           00001000111100011001101101010110
Astatini              001100001001000001000000000010
Pemphredonini         00110-010000100- - - - 0-0-100001
Psenini               -01-01001-0-0100141000010000 0
Mellinini             100100001-001020210000000100110
Palarini              001101001101010000-300001102010
Miscophini            10110-001-0-01000- 000000101 0- -
Larrini               - 0110-001-01-1000- 000001011010
Trypoxylini           10110-0010000100- - 0001001010- -
Crabronini            - 01-0-10110-0100- 000000101011
Oxybelini             101101101101010001000000101011
Alyssonini            10010-001101010200100000010 1000
Nyssonini             1011010101000000001-00000101000
Gorytini              100101001- - - 000001000000 1000000
Stizini               1011010-11-11000021-00-00110010
Bembicini             10-1010-11-1-100010000102 1-00-0
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                         3          4          5
Aphilanthopini        0001010010010100010000001 00010
Philanthini           000101001001010000000102100000
Cercerini             000-01001101101000100030101010
Colletidae            010101000100-100000001001 0-00-
Andrenidae            01-1010010010001000000010001000-
Halictidae            01-10100100010 00- 0000001010- -
Melittidae            0111010001001000000000001010000
Long-tongued Bees     011101000100010000-0-0010-0--
Laphyragogini         010100001101010000000001 00030
Xenospecini           011101001101000000000000100110
Dinetini              101101001001000000000000000011
Heliocausini          101101011001100000010000 0000000
Entomosericini        10110100100101100120000010 00000
Eremiaspheciini       101101001101010000000000 00000-0
Odontosphecini        00110100110101000000000100010 0
Pseudoscoliini        001101001001101-100-00000100000
Scapheutini           101101001001011011100100101010
Bothynostethini       101101001-0-1010000000001003000
Heterogyna            01000000110000000000000100 100031
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                         6          7          8
Outgroup 1 (Sphecos)  010000- 210100000- 0100000000000
Outgroup 2 (B and M)  000- 0020000000000000000000000
Outgroup 3 (optim.)   0100002000000000000000000000000
Ampulicini            12000002101001111120000000002
Dolichurini           010000021010011 1120000010002
Sceliphrini           0100102100100111120000000000
Sphecini              01001021001001111 2100000000000
Ammophilini           010010210010001111 2100000000000
Astatini              00000021101001110210101010-0010
Pemphredonini         02-0001210100111-21- - 011- - 0110
Psenini               010000-2101001112111011100110
Mellinini             0100000210100111210111103 0010
Palarini              1100001210100111 2101 1?1010110
Miscophini            00- 000-2101001111210111-020110
Larrini               -100002-0100111121011- - 020110
Trypoxylini           01000002-0100111121011110 20110
Crabronini            021000021010011 121011110 20110
Oxybelini             02100102-0100111121011110 1010
Alyssonini            01000002101001112101101111010 10
Nyssonini             0101000210100111210100111012
Gorytini              - - 0- - 0-210100111210100111011
Stizini               1101-0121010011121010011111011
Bembicini             - - 012002101001112101000011101-
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                         3          4          5
Aphilanthopini        010000121010011121110111- 1110
Philanthini           010000121010011121110111011110
Cercerini             010000-210100111211011120 11110
Colletidae            0-000020112111102010-0-00122
Andrenidae            0100002011211110210101 1-0122
Halictidae            01000020112111102101 01-01-1-2
Melittidae            01000012112111102101010-101-2
Long-tongued Bees     010-001-1121111021-00- - -10-02
Laphyragogini         00000022001 0?111121?????????0
Xenospecini           0100001210100111121 ?????????0
Dinetini              210100121010011112 1?????????0
Heliocausini          0100001210100111121?????????3
Entomosericini        0101001210100711121?????????1
Eremiaspheciini       0100012101007111 21?????????1
Odontosphecini        01000021010?111 21?????????1
Pseudoscoliini        01000012101001111 21?????????0
Scapheutini           110-00121010?111 21?????????2
Bothynostethini       010-00021010011 1121?????????0
Heterogyna            211000021010011112 1?????????0
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Table 2. Characters and character states used in the parsimony analyses. Characters marked with an asterisk were treated as nonadditive (= unordered).

Character
  Character States
0. Ocelli
    0. Hemispherical, with transparent lens
    1. Flattened, oval or linear, or reduced to a transverse scar
1. Inner margin of compound eyes
    0. More or less parallel
    1. Notched or emarginate
2.* Facets of compound eyes
    0. More or less uniform in size
    1. Some facets greatly enlarged ventrally or anteromedially
    2. Facets enlarged dorsally, very small ventrally
3. Stipes (on maxilla)
    0. Short and broad
    1. Long and narrow
4. Galea-glossa complex
    0. Short, broad, flap-like
    1. Moderately elongated, not flap-like
    2. Greatly elongated, subtubular
    3. Greatly elongated, flattened, enclosed ventrally by labial palpi, which have the basal two segments greatly elongated and flattened, the apical two segments much shorter, subcylindrical
5. Mandibular socket
    0. Open
    1. Closed
6. Labrum
    0. Short, wider than long, usually hidden by clypeus
    1. About as long as wide
    2. Longer than wide, extending well beyond clypeus
7. Externoventral tooth or notch on mandible
    0. Absent
    1. Present
8. Clypeus subdivided by distinct longitudinal lines
    0. No
    1. Yes
9*. Shape of clypeus
    0. Narrowly transverse
    1. Not transverse, but with a dorsally produced median portion
    2. Sharply rooflike (Ampulicini)
    3. Swollen, to accomodate proboscis when folded (Bembicini)
    4. Not transverse, but with a ventrally produced median portion
10. Gular area
    0. Narrow, so that hypostomal carina is close to occipital carina
    1. Broad, hypostomal carina widely separated from occipital carina
11*. Frontal carina
    0. Absent
    1. Present, evenly convex in profile, linear in frontal view
    2. Present, sharply angulate in profile, shaped like an inverted T in frontal view

    3. Present, a very broad ridge rather than a narrow carina (Nyssonini)
12. Frontal sulcus
    0. Absent
    1. Present
13. Antennal sockets
    0. Contacting clypeus, or separated from it by less than half the diameter of a socket
    1. Separated from clypeus by more than half the diameter of a socket
14. Subantennal sclerite delimited by subantennal sutures (= supraclypeal area of Michener, 1944)
    0. absent
    1. present
15. Clypeal brush   (in males only)
    0. absent
    1. present
16*. Propleuron
    0. Not specially modified
    1. Posterolateral margin lamellate, posterolateral angle declivous and set off from rest of propleuron by inner ridge or hump
    2. Anterior face flattened, somewhat compressed in lateral view, ventral margin and ventrolateral corner lamellate
17*. Pronotal collar
    0. Long, not collar-like
    1. Narrowly transverse, collar-like
    2. Evenly sloping from neck of pronotum up to scutum, so that there is no discernible collar (Astatini)
18. Pronotal lobe
    0. Contacting or nearly contacting tegula, so that scutum does not contact mesopleuron
    1. Separated from tegula by anterolateral process or carina from scutum, so that scutum directly contacts mesopleuron
19. Notauli
    0. Present, long
    1. Absent or very short (not reaching an imaginary line tangent to anterior margins of tegulae)
20*. Admedian lines of scutum
    0. Separate, distinct
    1. Fused into a single median line
    2. Absent
21. Oblique scutal carina
    0. Absent
    1. Present
22*. Scutellum
    0. Without lateral flange
    1. With lateral flange overlapping metanotum
    2. A horizontal, strap-like band tightly appressed to metanotum, posterior margin lamellate
23. Metanotal squamae
    0. Absent
    1. Present
24. Scutellum with a pitted transverse basal sulcus
    0. No
    1. Yes
25. Episternal sulcus
    0. Present, long (extending ventrad of scrobal sulcus)
    1. Short (not extending ventrad of scrobal sulcus) or absent

26. Omaulus
    0. Absent
    1. Present
27*. Postspiracular carina
    0. A narrow, sharp ridge forming the vertical anterior wall of the subalar fossa
    1. A broad, rounded ridge forming the vertical anterior wall of the subalar fossa
    2. Absent, because subalar fossa is absent or separated into anterior and posterior pits
28*. Subalar line
    0. Absent or incomplete, but subalar area not reduced
    1. Present, but not greatly expanded into a carinate ridge or flange
    2. Present as a very prominent carina or flange
    3. Absent, subalar area greatly reduced or absent
29*. Separation of middle coxae
    0. Metasternum quadrate or rectangular, on more or less the same plane as mesosternum, so that midcoxae are widely separated
    1. Similar to 0, but metasternum distinctly narrowed anteriorly, so that midcoxae are close together
    2. Metasternum on a different plane from that of mesosternum
30. Posterior margin of metasternum
    0. Broadly rounded, truncate, or weakly emarginate
    1. Bilobed, lobes subparallel and closely approximated
    2. Bilobed, lobes diverging apically
31. Precoxal lobes
    0. Present, delineated by distinct transverse groove from mesosternal apophyseal pit
    1. Absent
32. Dorsolateral carina on middle coxa
    0. Absent
    1. Present
33. Lower metapleural area
    0. Present
    1. Absent
34. Propodeal sternite
    0. Absent
    1. Present
35*. Propodeal enclosure
    0. Present, U-shaped
    1. Present, V-shaped
    2. Absent
36. Propodeal mucro
    0. Absent
    1. Present
37. Lateral spines or teeth on propodeum
    0. Absent
    1. Present
38. Tarsal claws
    0. Bifid or with subapical teeth or lobe
    1. Simple
39. Plantulae
    0. Present
    1. Absent
40. Apicoventral setae on hindtarsomere V
    0. Setiform
    1. Bladelike
41. Foretarsal rake (in females)
    0. Absent
    1. Present

42. Tarsomeres
    0. IV similar to III, V inserted toward apex of IV
    1. IV short, V inserted dorsally at base of IV
43. Number of midtibial spurs
    0. Two
    1. One
44*. Apex of hind femur
    0. Unmodified
    1. Broadened, truncate
    2. With an apical spatulate process
45. Insertion of metasoma
    0. Between hind coxae
    1. After and above hind coxae
46*. Metasomal petiole
    0. Absent
    1. Formed of first metasomal sternum only
    2. Formed of first metasomal sternum and first metasomal tergum
47*. Base of first metasomal sternum
    0. Simple, without any carinae
    1. With longitudinal median ridge or paired ridges
    2. With distinct transverse ridge
48*. Shape of second metasomal sternum
    0. Evenly convex, not swollen at base
    1. Swollen at base, but without a transverse sulcus
    2. Swollen at base, with a transverse sulcus at base of swollen area
    3. Palarini — varies between sexes and species, but usually a very prominent subapical transverse ridge (especially in males)
    4. Similar to state 2, but with a pair of basilateral nodes bearing tufts of very short, fine setae
49. Lateral line or carina on tergum 1
    0. Present
    1. Absent
50. Number of visible metasomal terga in males
    0. Seven
    1. Fewer than seven
51. Pygidial plate (in females)
    0. Present
    1. Absent
52*. Sixth metasomal sternum (females)
    0. Similar to other segments, except for troughlike vertical side walls
    1. Elongate, forming an exposed tapering tube through which sting is exserted
    2. Apically bifid or emarginate
53*. Apex of female metasoma
    0. More or less conical
    1. Strongly compressed laterally
    2. Strongly compressed dorsoventrally
54. Cerci (males)
    0. Present
    1. Absent
55. Laterobasal spiracular lobes on male tergum 7
    0. Absent
    1. Present
56*. Volsella
    0. With differentiated digitus and cuspis
    1. Digitus and cuspis fused, not differentiated
    2. Absent
    3. A large, rolled, C-shaped plate (Bothynostethini)
57. Penis valves (= "aedeagal head")

0. Without teeth on apicoventral edge
1. With numerous short teeth on apicoventral edge
58*. Apex of marginal cell
    0. Acuminate, ending on costal margin of wing
    1. Evenly truncate or broadly rounded
    2. Open (in some outgroup taxa)
    3. Obliquely truncate, not ending on costal margin of
       wing
59. Number of submarginal cells
    0. Three
    1. Two or fewer
60*. Forewing vein 3rs-m ("outer veinlet of 3rd submarginal
    cell" in Bohart & Menke, 1976)
    0. Ending near middle of marginal cell (= R1 cell)
    1. Ending near apex of marginal cell
    2. Absent
61*. Forewing vein 2-Rs ("outer veinlet of 1st submarginal
    cell" in Bohart & Menke, 1976)
    0. Angled, and with a remnant of vein 1r-rs (1st radial
       cross-vein)
    1. Straight or weakly curved, not appendiculate, no
       remnant of 1r-rs
    2. Absent
62. Number of discoidal cells in forewing
    0. Three
    1. Two or fewer
63. Divergence of forewing vein M
    0. At or after vein cu-a
    1. Before vein cu-a
64. Prestigmal length of 1st submarginal cell
    0. Less than twice height of cell
    1. Between two and three times height of cell
    2. More than three times height of cell
65. Submarginal and discoidal cells
    0. Separated by vein Rs+M
    1. Fused, due to loss of vein Rs+M
66. Jugal lobe
    0. Small or absent
    1. About 1/2 as long as vannal lobe
    2. More than 3/4 as long as vannal lobe
67. Hind wing vein 2A
    0. Present as a tubular vein
    1. Present as a nebulous or spectral vein
    2. Absent
68. Hind wing vein 3A
    0. Present
    1. Absent
69. Body vestiture
    0. Without plumose setae
    1. With at least some plumose setae
70. Female metasomal tergum 7
    0. Somewhat exposed, evenly sclerotized throughout
    1. Retracted and entirely hidden from external view,
       sclerotization reduced to a short strip across
       anterior margin
    2. Sclerotization entirely reduced mesally so that the
       lateral spiracular plates (hemitergites) are linked by
       membrane only
71. Female hind basitarsus
    0. Subcylindrical, about as wide as tarsomeres II - V
    1. Flattened, wider than tarsomeres II - V
72. Larval provisions
    0. Arthropods (usually paralyzed)

1. Pollen and nectar or plant oils
73. Posterolateral angle of pronotum
    0. Evenly rounded or subacute, reaching tegula
    1. Reduced dorsally above and slightly anterior to
       spiracular operculum; operculum forms a highly
       differentiated pronotal lobe
74. Ventral angle of pronotum
    0. Rounded, not much exceeding level of base of fore
       coxa
    1. Greatly produced, almost contacting its
       counterpart ventrally
75. Metapostnotum
    0. Forming a transverse groove at anterior margin of
       propodeum
    1. Greatly enlarged and posteriorly produced mesally,
       forming a "propodeal enclosure" or "propodeal
       triangle"
76. Hindtibial strigilus
    0. Absent
    1. Present
77*. Hind margin of pronotum
    0. Pronotum long, hind margin nearly straight, only
       very slightly anteriorly arcuate
    1. Pronotum shortened, hind margin strongly concave
       in a fairly regular and somewhat arcuate parabolic
       curve ("V-shaped")
    2. Pronotum shortened, hind margin shifted anteriorly
       over almost its entire width ("broadly U-shaped")
78. Prosternum
    0. Forming an approximately uniform plane, not
       sunken
    1. Sunken over most of its surface, only a short
       anterior section visible ventrally
79. Larval integument
    0. Smooth
    1. With abundant setae or dense spinules
80. Larval body shape
    0. With more or less even contours
    1. With conspicuous projections laterally, dorsally, or
       caudally
81. Position of larval anus
    0. Terminal, directed caudad
    1. Ventral, preapical, directed ventrad
82. Opening between atrium and sub-atrium of larval
    spiracles
    0. Armed with a circlet of spines
    1. Simple, unarmed
83. Parietal bands (on head of larva)
    0. Present
    1. Absent, or very faintly indicated
84. Larval antennal papillae
    0. Absent
    1. Present
85*. Larval mandibles
    0. Simple, with 4 or 5 apical teeth
    1. With fewer than 4 or 5 teeth
    2. With an apical concavity
    3. As in Mellinini (autapomorphy)
86. Larval maxillae
    0. Directed mesad apically, closely associated with
       labium and hypopharynx
    1. Projecting apically as large, free lobes
87. Larval galea

0. Large
2. Small
88*. Larval spinneret
  0. A transverse slit
  1. With paired openings, each at the end of a
    projection
  2. Absent
89. Male metasomal sternum 7
  0. Well developed, not much smaller than sternum 6,
    usually clearly visible externally and exposed
  1. Reduced and much smaller than sternum 6, but
    partly exposed
  2. Greatly reduced, much smaller than sternum 6 and
    completely hidden by it
  3. Absent

by Bohart and Menke are supported by the more rigorous analytical procedure described above. Table 3 lists the seven characters for which the optimization procedure results in a different polarity assessment from that hypothesized by Bohart and Menke. There are an additional twelve characters for which one procedure yields uncertain or equivocal results, whereas the other hypothesizes a single unequivocal groundplan state. Thus, a total of nineteen characters do not receive identical polarity codings with each procedure.

A few of the optimized polarity decisions are at odds with rather widely accepted ideas about character evolution in sphecid wasps and bees. Especially noteworthy in this respect are the episternal sulcus (character 25), plantulae (character 39), and foretarsal rake (character 41).

Bohart and Menke hypothesize that an episternal sulcus extending ventrad of the scrobal sulcus is the plesiomorphic condition for the Sphecidae, and bee systematists have generally regarded this character state as plesiomorphic for bees. For both groups, the basis of this assessment seems to be that a long episternal sulcus is present in taxa which generally have plesiomorphic states for other characters. Most taxa outside the Apoidea have no sulcus at all in the position of the episternal sulcus, but some Bethylidae (e.g. *Epyris clarimontis*) may have one. My analyses use Bohart and Menke's coding of "episternal sulcus absent or short" (Character 10 in their Table 2, p. 30; Character 25, state 1 in my Table 2) as a single character state. Under this coding, outgroup taxa are scored as having the episternal sulcus absent (or variable in Bethylidae), and the character state optimization procedure infers that the ancestor of the Apoidea had the episternal sulcus "absent or short". If

Table 3. Characters for which Bohart and Menke (1976) postulated different groundplan states from those derived by an optimized fit to a cladogram of aculeate taxa based on the studies of Brothers (1975) and Carpenter (1990), using the optimization procedure presented by Maddison et al. (1984). Characters and character states are defined in Table 2, and are merely given brief labels here. The column labelled "B & M" shows the groundplan state postulated by Bohart and Menke. This column corresponds to Outgroup 2 in Table 1. A "?" indicates that Bohart and Menke expressed doubt as to the plesiomorphic condition for the character, or did not indicate what they considered the plesiomorphic state to be. The column labelled "Optimized" shows the state assigned to the ingroup node (i.e. the state present in the ancestor of the Apoidea) as determined by the optimization procedure mentioned above. This column corresponds to Outgroup 3 in Table 1. Characters in this column denoted by a (B) are ones that Brothers used in his study, so that groundplan states for these characters are based upon his polarity assessments rather than the tree-fitting procedure of Maddison et al. (1984). Characters denoted by a "-" in this column and the "Sphecos" column are those for which polarity decisions were indecisive. The column labelled "Sphecos", equivalent to Outgroup 1 in Table 2, shows the groundplan states used in a preliminary analysis that I published in the newsletter Sphecos (Alexander, 1990). In that analysis, I did not distinguish between characters in my data matrix that had and had not been used by Brothers in his study. Instead, the groundplan state of each character was determined by optimizing its fit to Brothers' cladogram, regardless of whether or not the character had been used to derive the cladogram.

Character	Sphecos	B&M	Optimized
7. Mandibular notch	0	?	0
10. Gular area	-	0	0
12. Frontal sulcus	0	1	0
24. Scutellar sulcus	-	0	0
25. Episternal sulcus	1	0	1
29. Separation of midcoxae	0	?	1 (B)
31. Precoxal lobes	-	?	1
33. Lower metapleural area	-	0	0 (B)
39. Plantulae	-	0	1
41. Foretarsal rake	0	1	0
45. Insertion of metasoma	0	?	0
47. Base of sternum 1	-	0	-
49. Lateral line on tergum 1	-	1	-
61. Forewing vein 2-Rs	1	0	1
63. Divergence of vein M	0	?	0
66. Jugal lobe	-	2	2 (B)
67. Hind wing vein 2A	2	0	0 (B)
68. Hind wing vein 3A	1	0	0 (B)
76. Hindtibial strigilus	-	0	0

"absent" and "short" were coded as separate character states, the groundplan state for Apoidea would be equivocal, because the ingroup would have two derived states, neither of which occurs in the outgroup.

A similar argument explains the hypothesis that the absence of a foretarsal rake in females is plesiomorphic. In the outgroup taxa that I have examined, only Anthoboscinae and some Pompilidae have a foretarsal rake. In Brothers' original (1975) analysis, Apoidea and Vespoidea are sister taxa, and the first clade to branch off within Vespoidea is (Tiphiidae [with Anthoboscinae as the basal group] + (Sapygidae + Mutillidae)). In Carpenter's (1990) reanalysis of Brothers' data, Sierolomorphidae is the basal clade in Vespoidea. Females of Anthoboscinae, and some Sapygidae I have examined for this character (e.g. *Fedtschenkia anthracina*), have a foretarsal rake. Thus, if Brothers' original hypothesis of aculeate relationships is correct, the ancestral state of the foretarsal rake in Apoidea would be equivocal. Carpenter's cladogram supports the conclusion that the ancestor of Apoidea had no foretarsal rake.

In the outgroup, I find plantulae to be present in Pompilidae, Anthoboscinae, and some Rhopalosomatidae. Such a distribution results in the hypothesis that plantulae are primitively absent in Apoidea if Carpenter's cladogram is used. If Brothers' cladogram is used, the groundplan state for Apoidea is equivocal.

With the basic data matrix of Table 1, I have performed analyses to examine the effects of altering three variables: the taxa examined, the characters employed, and the groundplan character states for the hypothetical ancestor. The two different groups of taxa considered are (1) only those for which both adults and larvae have been described, and (2) all sphecid tribes, including those for which only adults are known. Including taxa for which only adults are known in an analysis that uses larval characters results in a data matrix with numerous "empty" cells (denoted by a "?" in Table 1). Although I use a parsimony program (Hennig86) that can analyze a matrix with missing information, the usual result of doing such an analysis is poorer resolution of phylogenetic relationships. The alternative is to completely ignore certain taxa because of insufficient information about them. Neither approach is completely satisfactory. By comparing the results of both approaches, one can at least find out if there are any patterns of phylogenetic relationships supported by both sets of incomplete information.

A similar rationale explains why I wish to compare the results of analyses that use both adult and larval characters with the results of analyses that use only adult characters. Finally, I examine the results of using a hypothetical ancestor based upon

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Table 4. Combinations of variables employed in the quantitative cladistic analyses. For hypothetical ancestor codings, the column labelled "Literature" utilized codings hypothesized in the literature, primarily by Bohart and Menke (1976) and Evans (1959), and the column labelled "Optimized" utilized codings based upon the procedures described by Maddison et al. (1984), as explained in the text. For each of the analyses designated by number in the table, there was also a part (a) in which all characters were given equal weight, and a part (b) in which successive approximations character weighting was used. Thus, Analysis 1b used hypothetical ancestor codings based on the literature, only sphecid tribes whose larvae are known, adult and larval characters, and successive approximations character weighting.

	HYPOTHETICAL ANCESTOR CODINGS	
TAXA EMPLOYED	LITERATURE	OPTIMIZED
Only sphecids whose larvae are known	**Analysis 1:** Adult & larval characters **Analysis 2:** Adult characters only	**Analysis 5:** Adult & larval characters **Analysis 6:** Adult characters only
All Sphecid Tribes	**Analysis 3:** Adult & larval characters **Analysis 4:** Adult characters only	**Analysis 7:** Adult & larval characters **Analysis 8:** Adult characters only

the polarity decisions of Bohart and Menke with the results of using a hypothetical ancestor based upon polarity decisions derived from character state optimization. This 2 x 2 x 2 arrangement of variables requires eight basic analyses. For each of these analyses, I also compare the results obtained when all characters are given equal weight with the results obtained when characters are weighted according to Farris' (1969) successive approximations procedure. Table 4 summarizes the combinations of variables used in each analysis.

As explained above, the assessments of character polarities made by Bohart and Menke agree with the results of a more formal analytical procedure for all but 19 of the characters included in the data matrix that I used. I therefore also examine the results of an analysis that excludes these 19 characters (the characters are listed in Table 3). For this analysis, I include all sphecid tribes and both adult and larval characters (except for the 19 characters just mentioned). The analysis including *Heterogyna* uses all sphecid tribes, adult and larval characters (the latter coded as unknown for *Heterogyna* and 10 other tribes), and the character state optimization procedure for outgroup analysis.

All analyses discussed below employed J.S. Farris' Hennig86 program, Version 1.5 (Farris 1988), and used the commands m* and bb* to search for the most parsimonious trees. Use of the bb* option was time-consuming, especially when numerous iterations were necessary in the successive approximations character weighting procedure. (According to Farris [1988], the bb command will not retain more than 100 minimum-length trees that are found in an extended branch-swapping procedure, whereas the bb* command will retain all minimum-length trees.) Comparison of results obtained with the bb and bb* commands for the same data set showed that they resulted in different weights assigned to some characters and thus different hypotheses of phylogenetic relationships. In view of this, I considered it preferable to use the more exhaustive branch-swapping procedure, under the assumption that it was taking complete account of all the available information, instead of using an arbitrary cut-off point in searching for multiple minimum-length trees.

In these analyses, the tribes of Sphecidae as defined by Bohart and Menke are used as the terminal taxa. This taxonomic level has been selected primarily for reasons of analytical tractabil-

ity. Bohart and Menke recognize 226 genera and 7,634 species of sphecid wasps, so even an analysis at the level of the genus would require an extremely large and cumbersome matrix. Grimaldi (1990) reported an attempt to analyze a matrix with 158 taxa in the dipteran family Drosophilidae using the Hennig86 program. He found that "initial runs ... using the complete matrix were never finished, so the matrix was gradually pared down until it was found that 127 taxa was the maximum number that the program could analyze (at least using the m*; bb commands)." The analytical tractability of a data matrix depends not only on the number of taxa, but also on the level of character conflict, with high levels of character conflict resulting in poor resolution, or multiple equally parsimonious resolutions. The results to be presented below show high levels of character conflict.

The major shortcoming of using tribes (or genera) as terminal taxa is that several of them are almost certainly paraphyletic, and treating such taxa as monophyletic adds yet another source of error and confusion in a phylogenetic analysis. Table 5 lists the tribes of sphecid wasps that are most likely to be paraphyletic, because they are defined by character states that Bohart and Menke themselves regard as plesiomorphic at the level of the tribe they define. Because of uncertainty about which tribes are monophyletic, a few of the characters in the matrix I used are autapomorphies. Although such characters are not useful for determining phylogenetic relationships among tribes, they do provide evidence that the tribe possessing them is monophyletic. Even with autapomorphies, the consistency indices for these analyses are low enough that anyone who erroneously tries to use this index as a measure of confidence in a phylogenetic hypothesis should be unlikely to develop a false confidence in these particular hypotheses.

RESULTS

Each of the analyses results in numerous equally parsimonious trees (range: 9 to 5,272 trees; tree statistics summarized in Table 6). Thus, the first conclusion is that these data provide support for a large number of competing hypotheses about phylogenetic relationships within the Apoidea. Figures 1-10 summarize the results of each analysis in a manner that facilitates comparison, although it is important to remember that the diagrams being compared are consensus trees, and that the actual

Table 5. Tribes in Bohart and Menke's (1976) classification that are defined by characters that they considered to be plesiomorphic at the level of the tribe.

TRIBE	COMMENTS
Sceliphrini	Apparently paraphyletic with respect to Sphecini + Ammophilini. Bohart and Menke interpreted the presence of plantulae in the Sphecinae as plesiomorphic, but the optimization procedure for establishing character polarity would interpret the presence of plantulae as an autapomorphy for Sceliphrini, although this character exhibits high levels of homoplasy.
Astatini	Includes all genera of subfamily Astatine except Dinetus.
Miscophini	Apparently paraphyletic with respect to other tribes of Larrinae.
Crabronini	Apparently paraphyletic with respect to Oxybelini.
Gorytini	Apparently paraphyletic with respect to other tribes of Nyssoninae.
Stizini	Apparently paraphyletic with respect to Bembicini.
Aphilanthopini	Apparently paraphyletic with respect to other tribes of Philanthinae.

Table 6. Summary statistics for the analyses defined in Table 4; C.I. = consistency index, R.I. = retention index. Analysis 9 used all sphecid tribes and both adult and larval characters, but excluded the nineteen characters listed in Table 3. "Heterogyna" refers to the analysis including the enigmatic genus *Heterogyna*.

		Length	C.I.	R.I.	No. of Trees
Analysis	1a	274	.44	.65	5272
	1b	726	.73	.84	108
Analysis	2a	242	.44	.63	42
	2b	633	.75	.83	99
Analysis	3a	346	.37	.60	3994
	3b	686	.72	.85	3994
Analysis	4a	314	.37	.58	3994
	4b	609	.70	.82	347
Analysis	5a	273	.44	.65	555
	5b	722	.73	.83	162
Analysis	6a	244	.44	.62	854
	6b	654	.77	.84	90
Analysis	7a	347	.37	.60	156
	7b	669	.72	.84	330
Analysis	8a	316	.37	.58	15
	8b	597	.70	.82	46
Analysis	9a	248	.41	.64	2009
	9b	570	.74	.86	3992
Heterogyna	a	356	.36	.60	351
	b	698	.68	.82	9

number of competing hypotheses is far higher than what is shown pictorially. Appendix 2 presents a brief discussion of the ambiguities involved in mapping character state distributions onto consensus trees.

Despite the large number of competing hypotheses that merit consideration, a few consistent patterns appear in all the analyses. Table 7 identifies groupings of terminal taxa that are consistently supported as monophyletic groups, and lists the characters that are always interpreted as synapomorphies for these groups. It seems reasonable to regard these groups as strongly supported by the available evidence, and it is noteworthy that most of them are groups that have long been regarded as "natural" and are similar or identical in composition to the subfamilies in Bohart and Menke's classification. Table 8 compares the monophyletic groups consistently supported in this study with the classification proposed by Bohart and Menke.

Just as noteworthy as the groupings of sphecid tribes that are consistently supported as monophyletic are traditional groupings that receive little or no support as monophyletic taxa. Judging from the results of these analyses, the subfamilies Pemphredoninae and Astatinae of Bohart and Menke's classification do not appear to be monophyletic. Each of these subfamilies consists of two tribes (one of the tribes of Astatinae is monotypic). Character states that Bohart and Menke use to unite these tribes into subfamilies appear to be plesiomorphic. The monophyly of each tribe was not investigated in this study.

One final general observation is that very few consistent and strongly supported patterns of relationships among major monophyletic groups within the Apoidea are found. In Figures 1-10, many of the internal branches are supported by very few characters, and most of these characters exhibit homoplasy.

The group of three tribes corresponding to Bohart and Menke's subfamily Sphecinae is consistently a basal lineage, and most of the remaining tribes share a substantial number of synapomorphies. The Ampulicinae of Bohart and Menke is a problematic group in this respect, however. In most of the analyses in which only adult characters are used, the Ampulicinae is placed in monophyletic groupings that also include several

Table 7. Groupings of terminal taxa that were consistently supported as monophyletic groups, and characters that were consistently hypothesized to be synapomorphies for each group. Character states are numbered as in Table 2.

AMPULICINAE (Ampulicini + Dolichurini)

24-1   Pitted transverse basal sulcus on scutellum (also occurs in nine other tribes, may vary within tribes).

28-2   Subalar line a very prominent carina or flange (also in Entomosericini).

30-2   Posterior margin of metasternum distinctly bilobed, lobes diverging apically.

48-2   Metasomal sternum 2 swollen at base, with a transverse sulcus or carina (also in Entomosericini).

50-1   Male with fewer than seven visible metasomal segments.

SPHECINAE (Sceliphrini + (Sphecini + Ammophilini))

5-1   Mandibular socket closed (also in Ampulicini, Pemphredonini, Scapheutini, most Philanthinae and bees, some Crabronini).

34-2   Propodeal sternite present (also in Dolichurini).

40-1   Apicoventral setae on hindtarsomere V bladelike (varies within Gorytini, Stizini, and Bembicini).

45-1   Insertion of metasoma after and above hind coxae (also in Dolichurini, according to Bohart and Menke).

46-1   Metasomal petiole formed of sternum 1 only (also in Psenini, and in some Pemphredonini, Trypoxylini, and Crabronini).

64-1   Prestigmal length of first submarginal cell less than twice height of cell (also in some Gorytini and Stizini).

Sphecini + Ammophilini

3-1   Stipes long and narrow (also in Palarini, Bembicini, Entomosericini, Xenosphecini, bees, most Philanthinae).

4-1   Galea-glossa complex long and narrow (also in Oxybelini, bees except Colletidae).

6-1   Labrum subquadrate.

13-1   Antennal sockets separated from clypeus by more than half the diameter of the socket (also in Psenini, Stizini, Laphyragogini, Odontophecini, Xenosphecini, bees, most Philanthinae, some Trypoxylini and Gorytini).

APIFORMES (Bees)

20-1   Admedian lines of scutum fused into a single median line

27-1   Postspiracular carina a broad, rounded ridge forming the vertical anterior wall of subalar fossa (interpreted as a reversal in these analyses).

38-0   Tarsal claw bifid or with subapical teeth or lobes (interpreted as a reversal in these analyses).

41-0   Foretarsal rake absent (interpreted as a reversal in these analyses).

69-1   Body vestiture including some plumose hairs.

70-2   Female metasomal tergum 7 divided into hemitergites.

71-1   Female hind tarsus flattened, wider than more distal tarsomeres.

72-1   Larval provisions consist of pollen and nectar or plant oils.

89-2   Male metasomal sternum 7 greatly reduced, much smaller than sternum 6 and completely hidden by it.

88   Larval spinnerets: variable, but never with paired openings, each at the end of a projection, so this character is interpreted as undergoing reversal in these analyses. (By comparison, Lomholdt (1982) interpreted the absence of paired spinnerets in bees as plesiomorphic.)

PHILANTHINAE s. str. (Aphilanthopini, Philanthini, Cercerini, Pseudoscoliini)

15-1   Male with a clypeal brush.

32-0   Middle coxae without a dorsolateral carina or crest (interpreted as a reversal in these analyses).

86-1   Larval maxillae projecting apically as free lobes (also in Nyssoninae).

APIFORMES + PHILANTHINAE

14-1   Delimited subantennal sclerite

NYSSONINAE s.str. (Nyssonini, Gorytini, Stizini, Bembicini)

21-1   Oblique scutal carina (in all analyses except 8b, in which these tribes are a paraphyletic assemblage).

82-0   Opening between atrium and subatrium of larval spiracles armed with a circlet of spines (interpreted as a reversal in these analyses).

Stizini + Bembicini

16-2   Propleuron with anterior face flattened, somewhat compressed in lateral view, ventral margin and ventrolateral corner lamellate

AMPULICINAE + SPHECINAE
(sister taxa only in Analyses 3b, 5b, 6b, and 7b)

9-1   Clypeus not transverse, but with dorsally produced median portion (further modified in Ampulicini)

52-1   Female metasomal sternum 6 elongate, forming an exposed tapering tube through which sting is exserted.

57-1   Penis valves with small teeth on ventral edge.

76-1   Hindtibial strigilus present (also present in most other Apoidea except Apiformes).

tribes traditionally assigned to the Nyssoninae.

Such a relationship has been suggested before, on the basis that the scutum overlies the tegula (Pate 1938), although Pate himself expressed reservations about this relationship. Most sphecid workers have not accepted the hypothesis of a close relationship between the Ampulicinae and Nyssoninae. It is worth noting that in the analyses hypothesizing that the Ampulicinae are part of the Nyssoninae (usually the sister group of Nyssonini), none of the putative synapomorphies for these taxa are unique to them. The characters consistently hypothesized as synapomorphies are presence of an omaulus (character 26-1 in Table 2); loss of a foretarsal rake (41-0, shared by Ampulicinae

Table 8. A comparison of Bohart and Menke's (1976) subfamilial classification of sphecid wasps with tribal groupings that were consistently hypothesized as monophyletic in this study. Monotypic subfamilies in Bohart and Menke's classification are not listed here, because in this study they were assumed to be monophyletic by definition.

BOHART AND MENKE	THIS STUDY
AMPULICINAE (tribes Ampulicini and Dolichurini)	Same as in Bohart & Menke
SPHECINAE (tribes Sceliphrini, Sphecini, and Ammophilini)	Same as in Bohart & Menke
PEMPHREDONINAE (tribes Psenini and Pemphredonini)	Monophyletic group only in consensus trees from Analyses 7a and 8a.
ASTATINAE (tribes Astatini and Dinetini)	Not a monophyletic group in any consensus trees.
LARRINAE (tribes Larrini, Palarini, Miscophini, Trypoxylini, Bothynostethini, and Scapheutini)	A monophyletic group of only these tribes was not consistently supported in all analyses, but many tribes of Bohart & Menke's Larrinae and Crabroninae frequently formed a monophyletic assemblage. The assemblage sometimes also included Alyssonini, Mellinini, and/or Heliocausini, and Larrini and Palarini were sometimes *not* included with the other tribes.
CRABRONINAE* (tribes Crabronini and Oxybelini)	*Menke (1988) now advocates including Oxybelini and Crabronini with the Larrinae, and no longer recognizes the subfamily Crabroninae.
NYSSONINAE (tribes Mellinini, Heliocausini, Nyssonini, Alyssonini, Gorytini, Bembicini, Stizini)	The tribes Nyssonini, Gorytini, Stizini, and Bembicini consistently formed a monophyletic assemblage, although this assemblage sometimes also included Ampulicini, Dolichurini, Entomosericini, and/ or Psenini.
PHILANTHINAE (tibes Eremiaspheciini, Philanthini, Aphilanthopini, Odontosphecini, Pseudoscoliini, Cercerini)	Aphilanthopini, Philanthini, Pseudoscoliini, and Cercerini consistently formed an exclusive monophyletic assemblage. Eremiaspheciini and Odontosphecini were never included in this assemblage.

and Nyssonini, the latter group consisting of cleptoparasites); hind wing jugal lobe small or absent (66-0); and male metasomal sternum 7 greatly reduced and hidden by sternum 6 (89-2). In analyses that hypothesize a sister group relationship between Ampulicinae and certain Nyssoninae, the ancestor of Ampulicinae is required to undergo numerous character state reversals, including loss of the oblique scutal carina (21-1). This character is unique to the tribes Bembicini, Gorytini, Nyssonini, and Stizini, which means that in this study it is a major character supporting the monophyly of these four tribes as a group ("Nyssoninae" in a narrow sense). The carina is not present in all members of Gorytini. Because this tribe is paraphyletic, the phylogenetic significance of the absence of the carina in some gorytine genera is unclear.

Many of the analyses in which both adult and larval characters are used hypothesize a sister group relationship between the Ampulicinae and the Sphecinae. Although Evans (1959, 1964) emphasizes the similarities in the larvae of these two groups, these similarities are features that he considers plesiomorphic, and in my analyses all the characters suggesting a sister group relationship between the two groups are features of adult morphology. The most frequently hypothesized synapomorphies are the dorsally produced clypeus (9-1), female metasomal sternum 6 forming a tube through which the sting is exserted (52-1), toothed penis valves (57-1), and presence of a hindtibial strigilus (76-1, also present in most other sphecids, but independently derived in Ampulicinae + Sphecinae if they are sister taxa).

Apart from the basal position of the Sphecinae

(and probably the Ampulicinae), the other consistent result of these analyses is a close relationship between the bees and the Philanthinae (i.e tribes Aphilanthopini, Cercerini, Philanthini, and Pseudosoliini — the tribes Eremiaspheciini and Odontosphecini, which Bohart and Menke placed in the Philanthinae, do not form a monophyletic grouping with these other four tribes in my analyses). In analyses that include all sphecid tribes, one or more of the following tribes are occasionally included in a monophyletic group that also contains the bees and Philanthinae: Psenini, Pemphredonini, Laphyragogini, and Xenospheciini (the last two tribes each contain one genus). Only one character is consistently hypothesized as a synapomorphy of bees and philanthines in all the analyses. This is a feature referred to by Bohart and Menke as a "delimited subantennal sclerite", which is equivalent to what bee specialists (following the terminology of Michener 1944) call the "supraclypeal area", and is not the same as Michener's "subantennal area". Perhaps it would be less confusing to think of this character in terms of the presence or absence of a subantennal suture extending from the dorso-lateral angle of the clypeus toward the antennal socket. Other characters hypothesized as synapomorphies of bees and philanthines in some, but not all, of the analyses are: elongated stipes (character 3-1), a closed mandibular socket (5-1), antennal sockets not contacting the clypeal margin (13-1), subalar line present but not specially modified (28-1, interpreted as a reversal when hypothesized as a synapomorphy), and larval mandibles with a reduced number of apical teeth (85-1).

One other way to summarize the results of these analyses is to consider the performance of individual characters. Apart from autapomorphies (either at the level of terminal taxa or of the Apoidea as a taxon), which can never support conflicting phylogenetic hypotheses, there are some characters that consistently support the same hypotheses in all analyses, and others that perform quite erratically. The successive approximations character weighting procedure takes this into account by assigning weights to characters according to their level of homoplasy in a parsimony analysis. Consequently, one way to summarize a complex body of information about character performance in a series of parsimony analyses is to compare the final weights assigned to each character in each analysis. Table 8 provides such a summary for the characters used in this study.

DISCUSSION

In the title of this paper, I have described this study as "exploratory". It is based upon definitions of characters and character states that are not well suited for cladistic analyses because they confound two different ways of thinking about character evolution, viz. homology and degree of divergence from an ancestral condition. Both types of character change are clearly part of evolution, but in order to properly describe either one, it is important to distinguish between them. In their tables, Evans, Bohart, and Menke treat all derived character states as equivalent, even in cases where it is very unlikely that they consider them homologous. For example, Bohart and Menke's definition of character states for the mouthparts (their Table 2, p. 30) is "mouthparts short" (plesiomorphic) and "mouthparts elongate or unusually modified" (apomorphic). If this is coded as a simple two-state character, as in Bohart and Menke's table, and used in a quantitative parsimony analysis, one is hypothesizing that the elongate mouthparts of Bembicini, in which the galea and glossa are lengthened but the stipes and prementum are relatively unmodified, are homologous to the elongate mouthparts of Philanthinae, in which the galea and glossa are short but the stipes and prementum are lengthened. Bohart and Menke did not intend their table to be interpreted in this way (A.S. Menke, personal communication), and my analysis makes some preliminary attempts to redefine their characters in a way that comes closer to identifying similarities that are likely to be homologous. However, there is a great need in sphecid systematics for careful comparative morphological studies such as the work on bee mouthparts that has been published in recent years, which has had the explicit goal of identifying homologous character states (Winston 1979, McGinley 1980, Michener and Brooks 1984; also see Bohart and Menke 1976 p. vii).

Neither a cladist nor an evolutionary taxonomist ever knows with absolute certainty whether or not a given shared similarity is really a synapomorphy. This is why parsimony analyses are done (Farris 1983). However, it does seem likely that a character analysis explicitly intended to distinguish between homologous and homoplastic similarities might do so more effectively than a character analysis that considers both types of similarity equally informative. A parsimony analysis utilizing the data that are supposed to form the basis of our existing

Table 9. Descriptive statistics for the weights assigned to each character by the successive approximations procedure in Analyses 1-9. Characters marked with an asterisk were not used in Analysis 9.

Character	Weight Mean	Weight Median	Weight Range
0. Ocelli	0.89	0	0-2
1. Inner margins of eyes	0	0	always 0
2. Eye facets	0.89	1	0-2
3. Elongated stipes	0.56	1	0-1
4. Galea-glossa complex	1	1	always 1
5. Mandibular socket	0.44	0	0-1
6. Labrum	3	3	always 3
*7. Mandibular notch	5	5	0-10
8. Tripartite clypeus	10	10	always 10
9. Shape of clypeus	3.67	3	3-5
*10. Gular area	10	10	always 10
11. Frontal carina	10	10	always 10
*12. Frontal sulcus	2.50	0	0-10
13. Antennal sockets	1.33	1	1-2
14. Subantennal sclerite	2.78	2	1-4
15. Male clypeal brush	9.11	10	2-10
16. Propleuron	4.56	3	2-10
17. Pronotal collar	2.67	3	1-4
18. Pronotal lobe	0	0	always 0
19. Notauli	0.89	0	0-2
20. Admedian lines	3	3	always 3
21. Oblique scutal carina	6.44	10	1-10
22. Scutellum	10	10	always 10
23. Metanotal squamae	10	10	always 10
*24. Scutellar sulcus	0	0	always 0
*25. Episternal sulcus	0.13	0	0-1
26. Omaulus	0.44	0	0-2
27. Postspiracular carina	1	1	always 1
28. Subalar line	1.33	1	0-3
*29. Separation of midcoxae	0.88	1	0-1
30. Metasternum	5.89	1	0-1
*31. Precoxal lobes	2.63	2	1-4
32. Midcoxal carina	0.33	0	0-1
*33. Lower metapleural area	0.75	0	0-2
34. Propodeal sternite	3	3	always 3
35. Propodeal enclosure	4.67	5	3-10
36. Propodeal mucro	10	10	always 10
37. Propodeal spines	0.44	0	0-2
38. Tarsal claw	1.67	2	1-2
*39. Plantulae	0	0	always 0
40. Setae on hindtarsomere V	10	10	always 10
*41. Female foretarsal rake	0	0	always 0
42. Tarsomere V	0	0	always 0
43. Midtibial spurs	1	1	0-2
44. Apex of hind femur	4	2	0-10
*45. Insertion of metasoma	10	10	always 10
46. Metasomal petiole	2	2	always 2
*47. Basal carina on S 1	2.13	2	1-3
48. Shape of sternum 2	6.67	4	4-10
*49. Lateral line on T1	2.75	3	1-3
50. Male metasomal segments	10	10	always 10
51. Female pygidial plate	0.67	1	0-1
52. Female sternum 6	7.78	10	5-10
53. Apex of female metasoma	0	0	always 0
54. Male cerci	0.33	0	0-1
55. Male tergum 7	7.78	10	0-10
56. Volsella	1	1	always 1
57. Teeth on penis valves	4.11	3	1-10
58. Apex of marginal cell	0	0	always 0
59. Submarginal cells	0.44	0	0-1
60. Forewing vein 3rs-m	0	0	always 0
*61. Forewing vein 2-Rs	0.38	0	0-1
62. Number of discoidal cells	10	10	always 10
*63. Forewing vein M	6.75	10	1-10
64. First submarginal cell	4	4	always 4
65. Vein Rs + M	10	10	always 10
*66. Jugal lobe	1.25	1	0-3
*67. Hind wing vein 2A	2.50	2	2-4
*68. Hind wing vein 3A	5.13	3	1-10
69. Plumose hairs	10	10	always 10
70. Female tergum 7	10	10	always 10
71. Female hind basitarsus	10	10	always 10
72. Larval provisions	10	10	always 10
73. Pronotum (posterolateral)	10	10	always 10
74. Pronotum (ventral angle)	10	10	always 10
75. Metapostnotum	10	10	always 10
*76. Hindtibial strigulus	2.25	2	2-4
77. Pronotum (hind margin)	10	10	always 10
78. Prosternum	10	10	always 10
79. Larval integument	7.20	10	3-10
80. Larval body shape	4	4	always 4
81. Position of larval anus	7.60	10	4-10
82. Larval spiracles	5.20	4	4-10
83. Larval parietal bands	1.80	2	1-2
84. Larval antennal papillae	1.80	2	1-2
85. Larval mandibles	3.20	3	2-4
86. Larval maxillae	3.60	4	2-4
87. Larval galea	6.40	4	4-10
88. Larval spinnerets	5	5	always 5
89. Male sternum 7	2.11	2	1-4

Autapomorphies of Apoidea: 18, 73, 74, 75, 77
Autapomorphies of terminal taxa: 8 (Palarini), 23 (Oxybelini), 36 (Oxybelini), 65 (Oxybelini)

phylogenetic hypothesis will reveal which characters support that hypothesis and which do not. As in any scientific investigation, further analysis can then be done to try to reconcile the conflicting evidence from the initial study.

It is also worth remembering that the groundplan states assigned to the hypothetical ancestor by the analytical procedure developed by Maddison et al. (1984) depend upon the validity of the phylogenetic hypothesis derived from the work of Brothers (1975) and Carpenter (1990). This is more than a trivial truism because the procedures that Brothers used to polarize characters in his analysis were, insofar as one can judge from his paper, essentially the same as those employed by Bohart and Menke. One respect in which his outgroup comparisons

may have differed from those of Bohart and Menke and Evans is that he seems to have placed special emphasis on a putative sister group of the Aculeata, the family Trigonalyidae (Brothers 1975 p. 491). The analyses presented in this paper show how sensitive phylogenetic hypotheses can be to polarity decisions for only a few characters in a data set, if that data set has high levels of character conflict. Until cladistic relationships among the major hymenopteran lineages are more completely understood, assigning groundplan character states for the Apoidea will remain problematic. This, in turn, will contribute to the difficulty of determining cladistic relationships within the Apoidea.

In my opinion, it is premature to propose any changes in the higher level classification of Apoidea on the basis of these analyses. I have nothing substantive to add to the long-standing debate about the merits of phenetic, cladistic, and more traditional classifications that attempt to combine cladistic and phenetic information. However, I will state for the record my preference for strictly cladistic classifications, in which only monophyletic (or holophyletic) groups are recognized and there is a direct correspondence between the classification and the branching pattern of phylogeny. Lomholdt's (1982) classification of sphecid wasps and bees is the only one known to me that has had these goals, but the analyses described in the present paper do not support the phylogenetic hypothesis upon which Lomholdt's classification is based. Indeed, my analyses demonstrate that no well-corroborated phylogenetic hypothesis for the sphecid wasps is yet available, so the necessary framework for a stable cladistic classification is also not yet available.

I do not consider the development of a sound phylogenetic hypothesis to be an unattainable goal, but the type of character analysis necessary to achieve this goal remains to be done. The major utility that I see for the analyses presented here is that they provide a starting point for studies aimed at developing a more rigorously formulated and more stable phylogenetic hypothesis upon which to base a classification. In particular, where monophyletic assemblages of tribes can be identified (Table 7), one can proceed to study relationships within these groups. For example, I have done such an analysis at the genus level for the "Philanthinae sensu stricto" of Table 7 (Alexander, 1992). Long-recognized groups whose monophyly is not supported by the evidence considered in this

paper (see Table 8) should be examined to determine if evidence for their monophyly has been overlooked or misinterpreted.

A long-standing and conspicuous disagreement about the higher level classification of sphecid wasps and bees centers upon the issue of which taxa should be assigned the rank of family (for example, compare Bohart and Menke 1976 with Krombein 1979). Cladists and evolutionary taxonomists use different criteria to resolve questions about taxonomic rank, and I will restrict myself to a consideration of rank from a cladistic perspective. Taxonomic rank in a cladistic classification simply indicates position in a branching sequence, and does not imply anything about overall phenetic similarity among taxa sharing the same rank. In a cladistic classification, a single family Sphecidae comprising all the Apoidea that are not bees is unacceptable, because it is clearly a paraphyletic group. If it could be shown that all of the taxa recognized as subfamilies in Bohart and Menke's classification are monophyletic, and that they are arrayed in a perfectly pinnate branching sequence, each taxon could be assigned the rank of family according to the sequencing convention of Nelson (1972). A different type of branching pattern would require a different combination of families and subfamilies. However, with our present dim understanding of phylogenetic relationships, it is unclear which of the groups of sphecid wasps that some recognize as families and others as subfamilies are even monophyletic, let alone what branching pattern links monophyletic groups. Tables 7 and 8 indicate that the evidence regarding the monophyly of these groups is mixed. From a cladistic perspective, the "one family vs. many families" debate over sphecid wasps amounts to a choice between a single family Sphecidae that is clearly paraphyletic or a mixed assemblage of smaller families, of which some are probably monophyletic and others not. The monophyly of bees is strongly supported, but the appropriate rank to assign them in a cladistic classification depends upon the branching pattern among the Apoidea that are not bees. This is not a satisfactory situation. It is a problem that needs to be addressed, if our classification is to serve as a powerful analytical tool rather than a source of confusion in our attempts to understand these beautiful and fascinating insects.

ACKNOWLEDGMENTS

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APPENDIX 1: TAXA EXAMINED

For the ingroup, species selected for studies of adult morphology were those used in Evans' studies of sphecid larvae, plus exemplars from tribes whose larvae have never been described.

OUTGROUP

ICHNEUMONOIDEA

Ichneumonidae: *Exeristes roborator, E. comstockii, Pimpla aequalis, Scambus brevicornis*

Braconidae: *Doryctes spp., Spathius spp., Helcon spp.*

CHRYSIDOIDEA

Plumariidae: *Plumaroides andalgalensis, Plumarius sp., Myrmecopterina sp.*

Bethylidae: *Epyris coriaceus, E. clarimontis, Anisepyris aurichalceus, A. subviolaceus, Pristocerus armifera*

Scolebythidae: *Clystopsenella longiventris*

VESPOIDEA

Sierolomorphidae: *Sierolomorpha ambigua, S. canadensis, S. nigrescens, S. similis*

Rhopalosomatidae: *Rhopalosoma nearcticus, Olixon banksii*

Pompilidae: *Auplopus (Lophagenia) erigone, Episyron biguttata, Priocnemoides fulvicornis*

Anthoboscinae: *Lalapa lusa, Plesiomorpha albinervis, Cosila chilensis, Anthobosca madecassa*

INGROUP

Andrenidae: *Andrena thaspii, Calliopsis andreniformis*

Halictidae: *Halictus rubicundus, Augochlora pura, Dufourea marginata, Nomia notiomorpha*

Melittidae: *Melitta leporina*

Colletidae: *Hylaeus basalis, Colletes wootoni*

Anthophoridae: *Exomalopsis albata*

Megachilidae: *Ashmeadiella californica, Megachile texana*

Ampulicini: *Ampulex canaliculata*

Dolichurini: *Dolichurus corniculus*

Sceliphrini: *Sceliphron caementarium, S. assimile, S. spirifex, Chalybion californicum, Chlorion aerarium, Podium rufipes, P. flavipenne, P. luctuosum*

Sphecini: *Prionyx atratus, P. thomae, Isodontia mexicana, I. philadelphica, I. auripes, I. elegans, Palmodes dimidiatus, Sphex ichneumoneus, S. pensylvanicus, S. argentatus, S. tepanecus*

Ammophilini: *Podalonia luctuosa, P. tydei, P. robusta, Ammophila procera, A. urnaria, A. harti, A. juncea, A. campestris, A. aberti, A. placida, A. pruinosa, A. fernaldi*

Dinetini: *Dinetus pictus*

Astatini: *Astata unicolor, A. occidentalis, A. minor, A. boops, A. bicolor, Dryudella immigrans*

Palarini: *Palarus variegatus*

Miscophini: *Miscophus bicolor, M. (Nitelopterus) evansi, M. (N.) slossonae barberi, Nitela spinolae, Plenoculus davisi, Solierella blaisdelli, S. peckhami, S. compedita*

Larrini: *Ancistromma distincta, Liris haemorrhoidalus, Li. nigra, Larra analis, La. luzonensis, Tachytes aurulentus, T. crassus, T. distinctus, T. mergus, Tachysphex apicalis, Tx. costa, Tx. obscuripennis, Tx. nitidus, Tx. pompiliformis*

Trypoxylini: *Pisonopsis birkmanni, Pison argentatum, P. atrum, Trypoxylon (Trypargilum) clavatum, T. (Tg.) collinum, T. (Tg.) politum, T. (Tg.) spinosum, T. (Tg.) tridentatum, T. (Tg.) texense, Trypoxylon (Trypoxylon) ashmeadi, T. (Tn.) figulus, T. (Tn.) frigidum, T. (Tn.) johnsoni*

Crabronini: *Anacrabro ocellatus, Crabro advenus, Cb. argusinus, Cb. monticola, Crossocerus annulipes, Cs. capitosus, Cs. cinxius, Cs. fergusoni, Cs. nigritus, Cs. podagritus, Cs. quadrimaculatus, Cs. walkeri, Ectemnius atriceps, E. cavifrons, E. continuus, E. guttatus, E. paucimaculatus, E. sexcinctus, E. stirpicolus, E. tumidoventris, E. zonatus, Entomognathus brevis, Lindenius pygmaeus, L. tylotis, Moniaecera asperata, Rhopalum clavipes, R. coarctatum, R. pedicellatum, R. rufigaster, Tracheliodes amu, T. quinquenotatus*

Oxybelini: *Oxybelus argentatus, O. bipunctatus, O. quadrinotatus, O. victor*

Bothynostethini: *Bothynostethus distinctus*, *Willinkiella argentina*

Scapheutini: *Bohartella scapheutoides*, *Scapheutes brasilianus*

Laphyragogini: *Laphyragogus pictus*

Xenosphecini: *Xenosphex timberlakei*, *X. xerophilus*

Entomosericini: *Entomosericus concinnus*, *E. kaufmani*

Heliocausini: *Heliocausus argentinus*, *H. fiebrigi*

Pemphredonini: *Ammoplanus handlirschi*, *Arpactophilus steindachneri*, *Diodontus minutus*, *D. tristis*, *D. virginianus*, *Microstigmus comes*, *Passaloecus clypealis*, *Pa. corniger*, *Pa. cuspidatus*, *Pa. eremita*, *Pa. gracilis*, *Pa. insignis*, *Pa. pictus*, *Pa. singularis*, *Pemphredon (Cemonus) gennelli*, *Pe. (C.) inornatus*, *Pe. (C.) lethifer*, *Pe. (C.) rugifer*, *Pe. (C.) wesmaeli*, *Pe. (Ceratophorus) morio*, *Pe. (Pemphredon) concolor*, *Pe. (P.) lugens*, *Pe. (P.) lugubris*, *Spilomena enslini*, *Stigmus fraternus*, *St. inordinatus*, *St. pendulus*, *St. solskyi*

Psenini: *Mimesa bicolor*, *Mimumesa nigra*, *Pluto albifacies*, *Psen ater*, *Psen bakeri*, *Psen simplicicornis*, *Psenulus fuscipennis*, *Psenulus pallipes*

Mellinini: *Mellinus arvensis*

Alyssonini: *Alysson melleus*, *A. cameroni*, *Didineis latimana*

Nyssonini: *Epinysson basilaris*, *Nysson daecki*, *N. trimaculatus*

Gorytini: *Gorytes canaliculatus*, *G. pleuripunctatus*, *Hoplisoides costalis*, *H. hamatus*, *H. placidus nebulosus*, *Ochleroptera bipunctata*, *Oryttus gracilis*, *Sphecius speciosus*

Stizini: *Bembecinus mexicanus*, *B. neglectus*, *B. tridens*, *B. quinquespinosus*, *Stizoides unicinctus*, *Stizus pulcherrimus*

Bembicini: *Bembix amoena*, *B. belfragei*, *B. cameroni*, *B. cinerea*, *B. comata*, *B. hinei*, *B. integra*, *B. multipicta*, *B. nubilipennis*, *B. occidentalis*, *B. oculata*, *B. olivacea*, *B. pallidipicta*, *B. sayi*, *B. spinolae*, *B. texana*, *B. troglodytes*, *B. dentilabris*, *Bicyrtes fodiens*, *B. quadrifasciata*, *B. ventralis*, *Glenostictia pulla*, *G. scitula*, *Microbembex monodonta*, *Rubrica nasuta*, *Steniolia duplicata*, *S. elegans*, *S. longirostra*, *S. obliqua*, *Stictiella formosa*, *S. pulchella*, *S. serrata*, *Stictia carolina*, *S. heros*, *S. signata*, *S. vivida*

Eremaspheciini: *Eremasphecium desertorum*, *E. schmiedeknechti*

Odontosphecini: *Odontosphex paradoxus*

Pseudoscoliini: *Pseudoscolia dewitzi*, *P. pharaonum*, *P. theryi*, *P. tricolor*

Aphilanthopini: *Aphilanthops foxi*, *A. frigidus*, *A. hispidus*, *A. subfrigidus*, *Clypeadon bechteli*, *C. californicus*, *C. dreisbachi*, *C. evansi*, *C. haigi*, *C. laticinctus*, *C. sculleni*, *C. taurulus*, *C. utahensis*, *Philanthinus integer*, *P. quattuordecimpunctatus*

Philanthini: *Philanthus albopilosus*, *P. barbiger*, *P. bicinctus*, *P. bilunatus*, *P. coarctatus*, *P. coronatus*, *P. crabroniformis*, *P. gibbosus*, *P. politus*, *P. solivagus*, *P. tarsatus*, *Trachypus mexicanus*, *T. petiolatus*

Cercerini: *Cerceris angularis*, *C. clypeata*, *C. flavofasciata floridensis*, *C. frontata frontata*, *C. fumipennis*, *C. nigrescens*, *C. robertsoni robertsoni*, *C. r. emmiltosus*, *C. rubida julii*, *C. sabulosa*, *C. quinquefasciata*, *Eucerceris bitruncata*, *E. flavocincta*

Heterogyna: *H. botswana*, *H. fantsilotra*, *H. madecassa*, *H. protea*

APPENDIX 2

On a strict consensus tree, polytomies usually mean that there are numerous equally parsimonious arrangements of the taxa involved in the polytomy. This creates difficulties for those wishing to present the evidential support for a consensus tree by mapping the distribution of character states upon the tree. It has even been argued that character states should not be mapped onto consensus trees (Nixon 1991). The following simple example is intended to explain how one might interpret the distributions of character states on the polytomies in the consensus trees in this paper. The simplest possible polytomy would involve three taxa and three characters. There are three possible cladograms for three taxa, and in this example each of the possible trees is supported by one character (a "1" in the data matrix represents the apomorphic character state). A strict consensus tree for this data set would be an unresolved trichotomy. The cladograms show how characters are distributed on each of the three equally parsimonious cladograms (all three cladograms have a length of 5 steps). If characters are mapped onto the strict consensus tree, each terminal taxon is depicted as having two autapomorphies, whereas in each of the fully resolved cladograms only one terminal taxon has two autapomorphies. In general, whenever two or more taxa involved in a polytomy on a consensus tree share a derived character state, that character state can be interpreted as a synapomorphy in one or more of the equally parsimonious cladograms that are represented by the polytomy. For example, characters 13, 14, and 15 in Fig. 1A are depicted as autapomorphies for the taxa Aphilanthopini, Philanthini, and Cercerini. Fig. 1A is a consensus tree for 5,272 equally parsimonious cladograms, and on many of these cladograms characters 13-15 would be synapomorphies for a monophyletic group containing the tribes Aphilanthopini, Philanthini, and Cercerini.

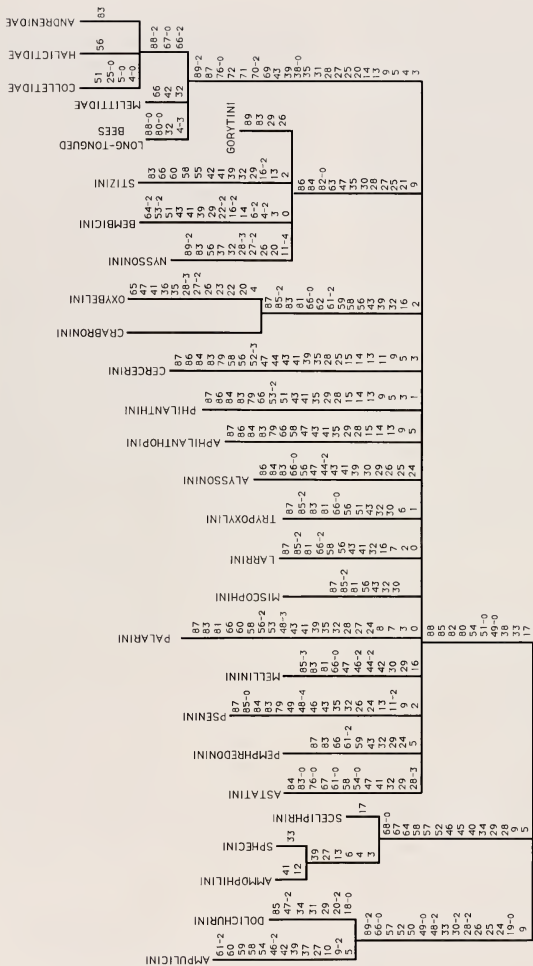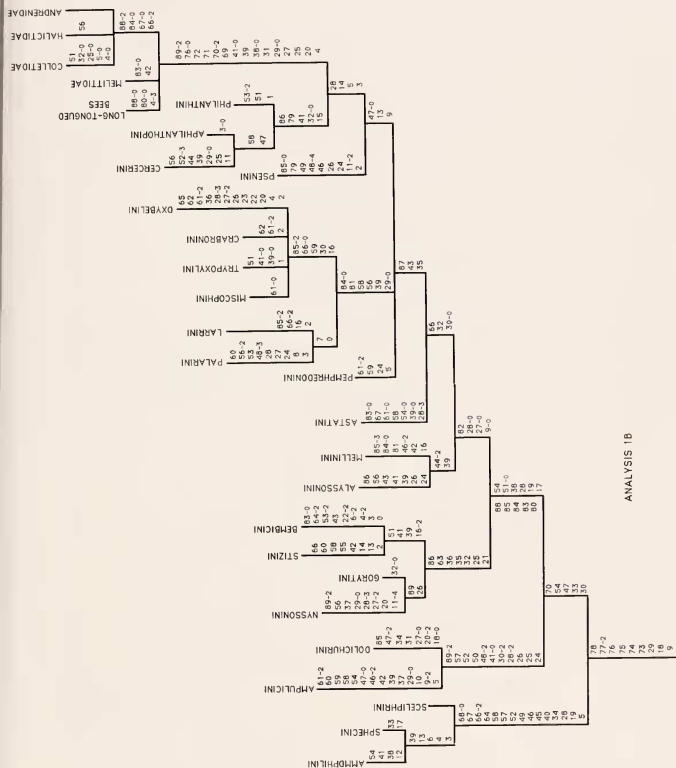| TAXON	CHARACTER 1	2	3
A	1	1	0
B	1	0	1
C	0	1	1
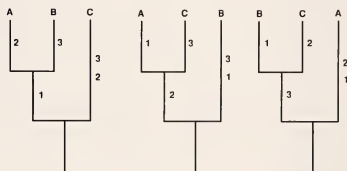
THREE EQUALLY PARSIMONIOUS CLADOGRAMS

STRICT CONSENSUS TREE
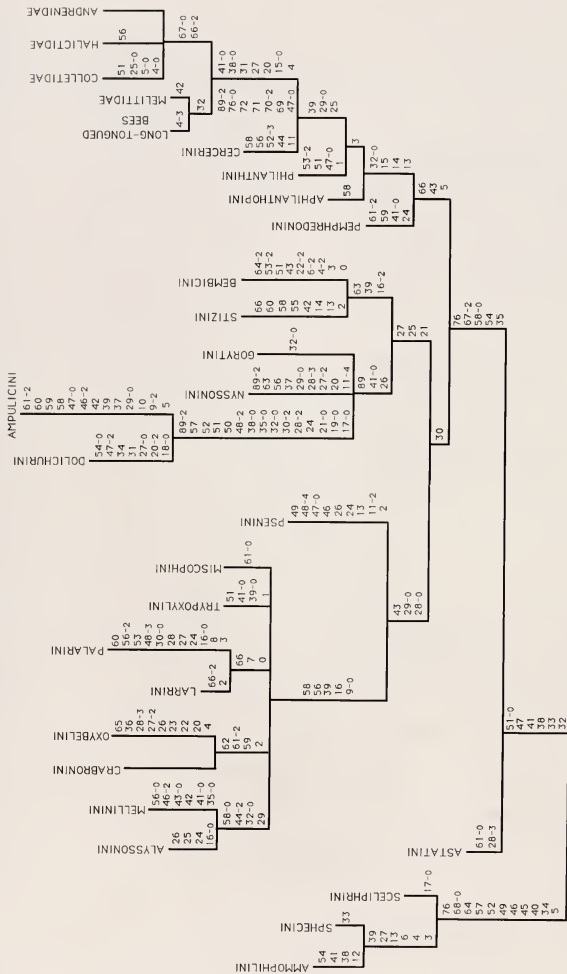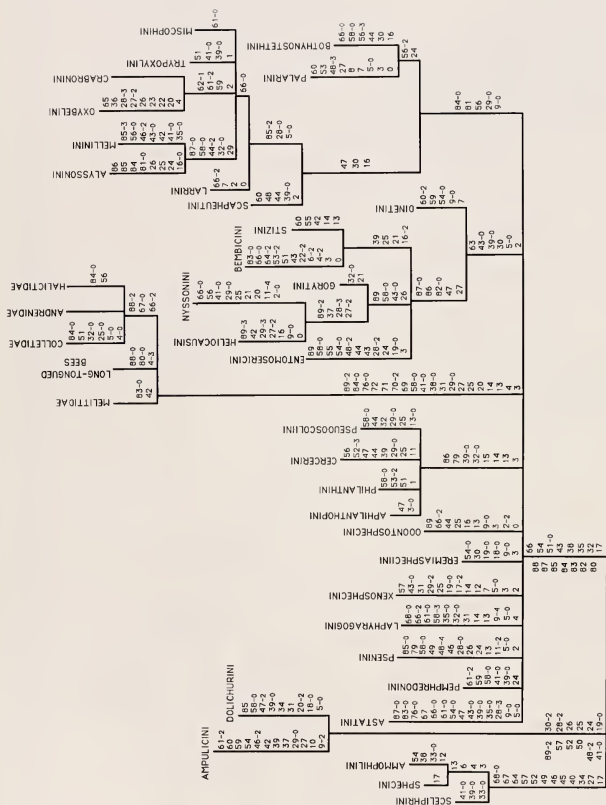
ANALYSIS 1A

Fig. 1. Strict consensus tree for Analysis 1 (adult and larval characters, tribes with unknown larvae excluded, polarities taken from the literature): (A) equal weights for all characters; (B) successive approximations character weighting. In Figs. 1–10, numbers on the branches correspond to the characters in Tables 1 and 2. Where a character number is shown without a subscript, it is implicitly hypothesized that a transition from state 0 to state 1 has occurred. Other character state transitions are identified by appropriate subscripts. Characters are not mapped on branches where more than one state may occur, either because more than one state would be equally parsimonious for a hypothetical ancestor, or because the character is coded as variable for a terminal taxon.

ANALYSIS 2A

Fig. 2. Strict consensus tree for Analysis 2 (adult characters only, tribes with unknown larvae excluded, polarities taken from the literature). (A) equal weights for all characters; (B) successive approximations character weighting.
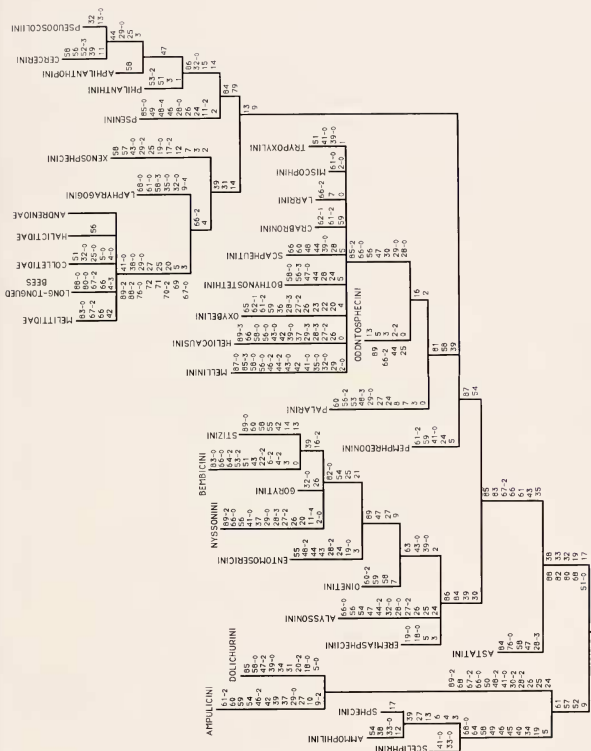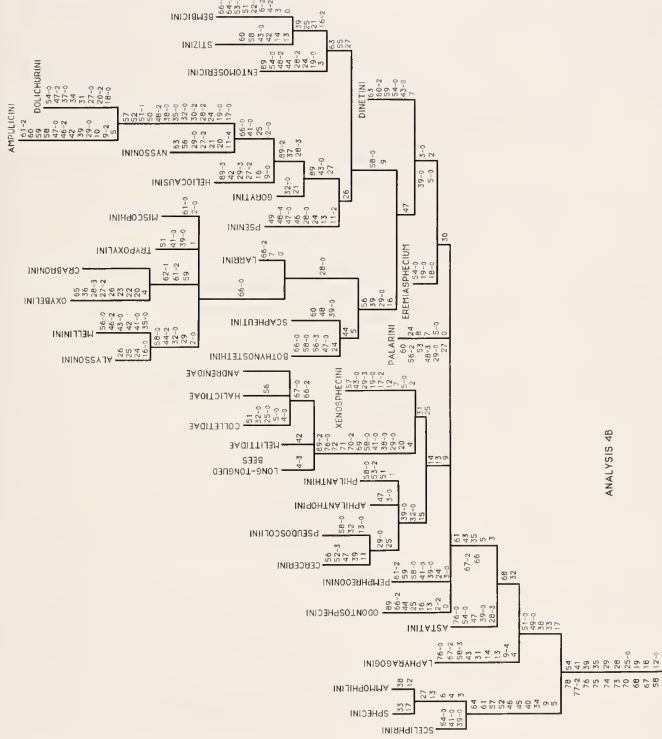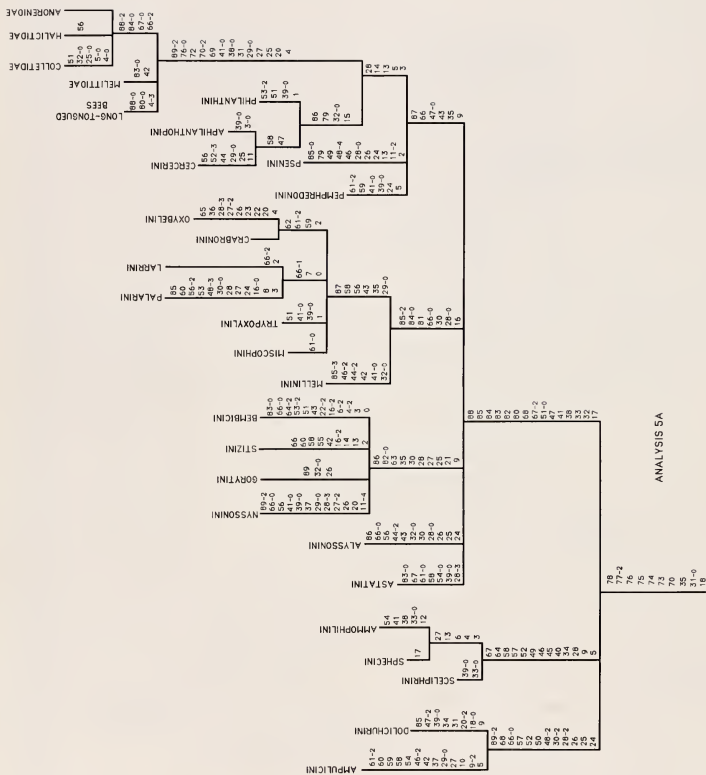
ANALYSIS 3A

Fig. 3. Strict consensus tree for Analysis 3 (adult and larval characters, all sphecid tribes, polarities taken from the literature): (A) equal weights for all characters; (B) successive approximations character weighting.
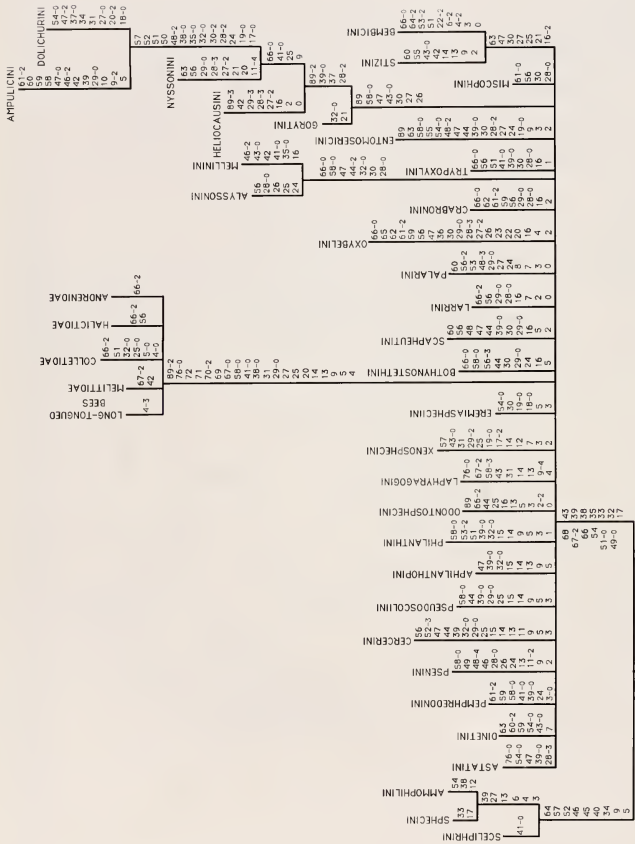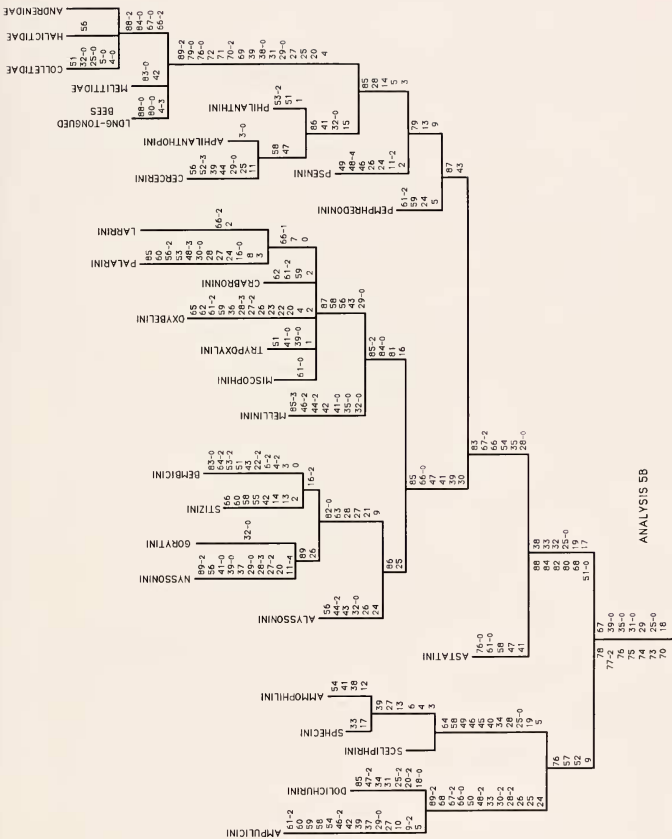
ANALYSIS 4A

Fig. 4. Strict consensus tree for Analysis 4 (adult characters only, all specid tribes, polarities taken from the literature); (A) equal weights for all characters; (B) successive approximations character weighting.
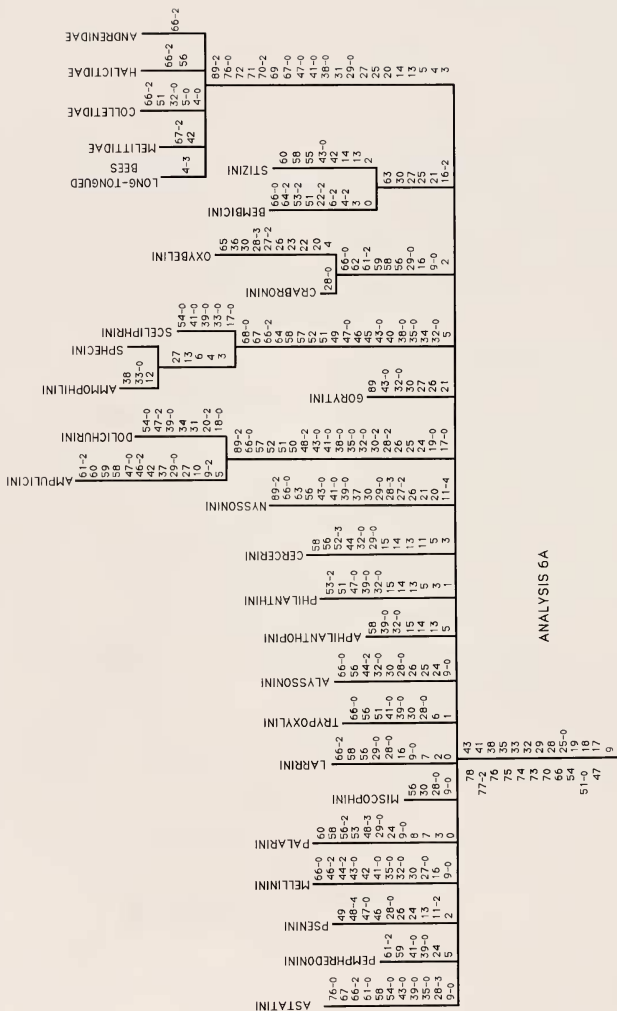
ANALYSIS 5A

Fig. 5. Strict consensus tree for Analysis 5 (adult and larval characters, tribes with unknown larvae excluded, polarities based on optimization); (A) equal weights for all characters, (B) successive approximations character weighting.
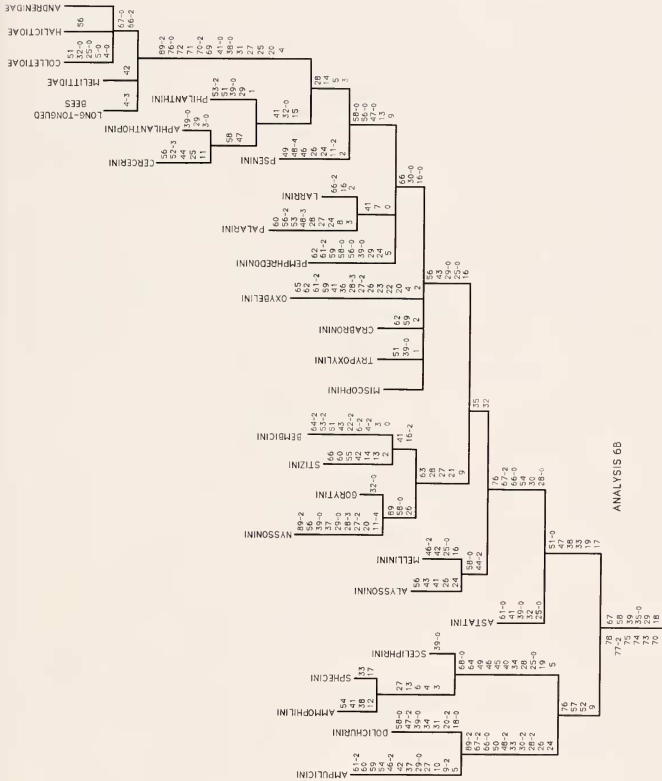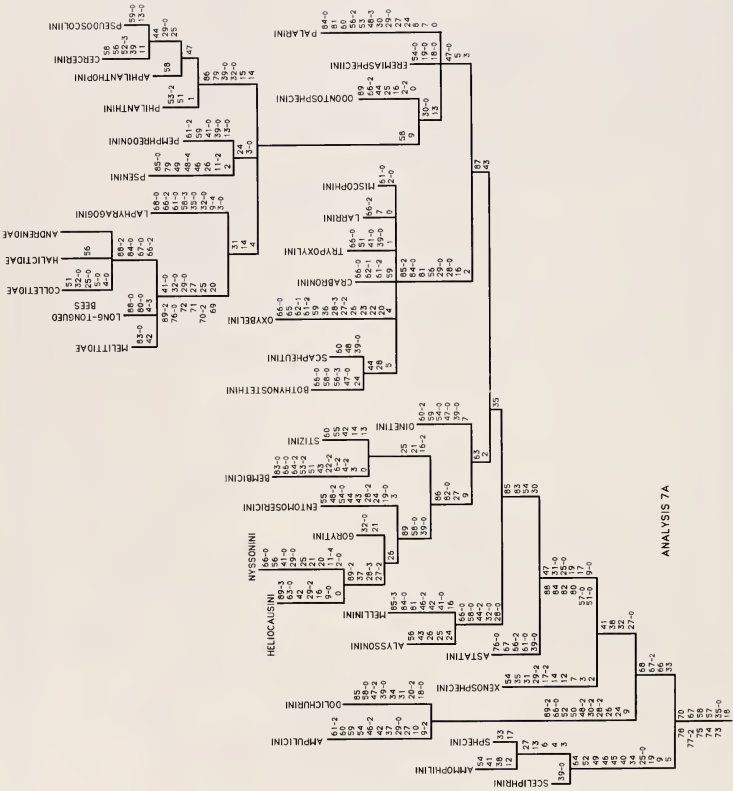
ANALYSIS 6A

Fig. 6. Strict consensus tree for Analysis 6 (adult characters only, tribes with unknown larvae excluded, polarities based on optimization); (A) equal weights for all characters; (B) successive approximations character weighting.
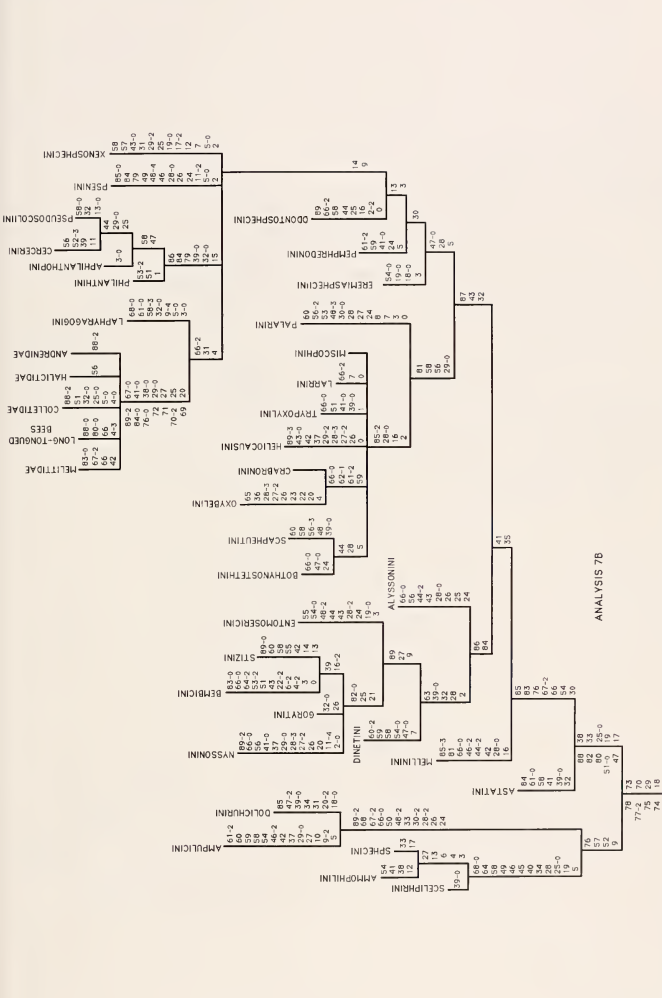
ANALYSIS 7A

Fig. 7. Strict consensus tree for Analysis 7 (adult and larval characters, all sphecid tribes, polarities based on optimization): (A) equal weights for all characters; (B) successive approximations character weighting.

ANALYSIS 8A

Fig. 8. Strict consensus tree for Analysis 8 (adult characters only, all sphecid tribes, polarities based on optimization); (A) equal weights for all characters; (B) successive approximations character weighting.

Fig. 9. Strict consensus tree for Analysis 9b (adult and larval characters, all spheciid tribes, polarities based on optimization, nineteen characters of especially doubtful polarity excluded, successive approximations character weighting).
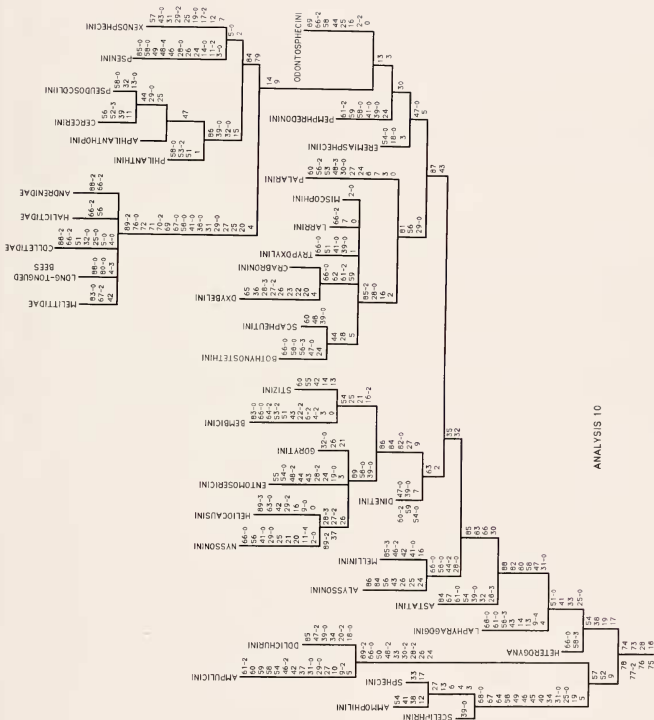
Fig. 10. Strict consensus tree for an analysis that included the genus *Heterogyna* (adult and larval characters, all sphecid tribes, polarities based on optimization, successive approximations character weighting).